

Brown bears selectively kill salmon with higher energy content but only in habitats that facilitate choice

Scott M. Gende, Thomas P. Quinn, Ray Hilborn, Andrew P. Hendry and Bobette Dickerson

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Pacific salmon return to spawn in thousands of streams across the Pacific Rim, from large rivers to tiny headwater streams. Once on the spawning grounds, salmon undergo dramatic biochemical changes as they metabolize stored lipid and protein reserves; at stream entrance, they will contain up to 85% more lipid and 40% more protein than at their senescent death a week or two later. Foraging brown and black bears that congregate at spawning streams thus encounter salmon that vary dramatically in their energy content and thus energetic reward. We hypothesized that bears would selectively kill salmon that are highest in energy content (fewest number of days on the spawning grounds) when they pursue salmon at small shallow streams where little effort is necessary to capture salmon, i.e. habitats that facilitate choice. In contrast, bears in environments where foraging is difficult (deeper, more complex streams) should be less selective and should capture salmon that are most available. We tested these ideas by examining predation rates on fish of different in-stream ages (i.e. energy content) at three different streams that varied in physical habitat attributes. At a very shallow, simple stream, bears preferentially killed salmon that had spent the fewest days in the stream. At two streams where deeper water and woody debris provided refuges for salmon, predation rates increased with in-stream age. At the shallowest streams encounter rates and capture success are likely equal among the high- and low-energy salmon and thus predation rates reflect active choice by bears. In contrast capture success probably increases on the older salmon at the larger streams (due to a loss of vigor), and thus 'preference' for these fish increases due to decreasing effort necessary to capture them.

S. Gende, Pacific Northwest Research Station, 2770 Sherwood Ln Suite 2A, Juneau, AK 99801, USA. Current address: National Park Service, Glacier Bay Field Station, 3100 National Park Road, Juneau, AK 99801, USA (scott_gende@nps.gov). – T. Quinn, R. Hilborn, and B. Dickerson, School of Aquatic and Fishery Sciences, Box 355020, Univ. of Washington, Seattle, WA 98195, USA. – A. P. Hendry, Redpath Museum and Dept of Biology, McGill Univ., Montreal, Canada, H3A 2K6.

When energy intake is closely coupled to fitness, foraging animals should select prey types that maximize their energy intake per unit foraging time (Stephens and Krebs 1986). However, detecting such selectivity has been difficult, particularly in a field setting, because prey types that vary in energy content may also vary in spatial distribution (including access to refuges), morphology (e.g. armor), chemical defenses (e.g. toxins), behavior

(e.g. daily movements, escape ability), and other features that influence the effort necessary for predators to capture them (Christensen and Persson 1993, Sih and Christensen 2001). Consequently, few field studies have been able to study prey selection by foragers in the absence of multiple confounding factors.

Each year around the Pacific Rim, brown bears (*Ursus arctos*) and black bears (*Ursus americanus*) congregate

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in riparian areas to feed on spawning salmon (*Oncorhynchus* spp.). This predator-prey relationship provides an excellent opportunity to study decisions by foragers pursuing prey that vary dramatically in energy content and therefore energetic reward. First, when bears seek and pursue salmon they simultaneously encounter fish that vary dramatically in energy content. Adult Pacific salmon do not feed in fresh water but accomplish upstream migration and spawning through the depletion of stored reserves of lipid and protein (Gilhousen 1980, Hatano et al. 1995, Hendry and Berg 1999). Between the start of spawning (when they first become vulnerable to bears) and senescent death, salmon will lose 80–95% of their lipid and roughly 40–50% of their total energy (Hendry and Berg 1999, Fig. 1). This physical deterioration inevitably leads to death, even in the absence of predation. Furthermore, bears can visually assess differences in energy content among salmon because these differences are accompanied by changes in skin pigmentation, body fungus, and wounds (Davis 1970, Brett 1995). Thus, bears simultaneously have access to multiple prey types (salmon varying in energy content) within the same habitat, and they can assess these differences.

Second, fitness of bears is strongly coupled to their energy intake in the fall prior to denning. Bears will lose 30–40% of their body mass while denning, and lipid stores accrued in the fall will be used to fuel metabolic and reproductive costs while in the dens (Atkinson and Ramsay 1995, Hilderbrand et al. 1999). Denning and reproduction (for females) is an energetically taxing process (Hilderbrand et al. 2000) and reproductive success is positively correlated with lipid reserves when

they enter dens in the fall (Stringham 1989, Miller et al. 1997). Lower fat reserves in bears at den entrance may influence fitness via aborted reproductive effort, or by the reduced survival of offspring in the spring following den emergence (Hilderbrand et al. 2000).

Finally, confounding factors associated with different prey types will be minimized because each individual fish will change in prey ‘type’ through its spawning life; high-energy fish just entering a stream will turn into low-energy fish after a few days to a week. Consequently, different prey types (high- vs low-energy salmon) will vary little in anti-predator morphology (e.g. spines or armor), toxins, venom or such other adaptations. Older salmon may be weaker and easier to capture but, in general, salmon show very little anti-predator behavior, except lateral escape in the stream, into deep pools, or under the shelter of large woody debris (tree trunks, roots, or tangles of branches). Moreover, different prey types will be found within the same habitat, often spawning next to each other. Salmon spawn in a variety of streams that vary dramatically in depth, flow, and amounts of woody debris (complexity), providing an opportunity to examine prey selection by bears in relation to the difficulty of prey capture.

In the present study, we made predictions of the selective foraging of brown bears (*Ursus arctos*) feeding on adult sockeye salmon (*Oncorhynchus nerka*) and pink salmon (*Oncorhynchus gorbuscha*) in different habitats (streams). Our objectives were (1) to quantify predation rates on salmon as a function of their in-stream age (a surrogate for energy content), (2) to determine whether bears selectively kill salmon with respect to in-stream age, and (3) to determine whether this selectivity varies among habitats. We addressed these objectives by examining daily rates of predation on fish of known in-stream age for up to four years in three different streams that varied in depth, width, and amount of woody debris. In habitats that facilitate choice (very small and simple streams), we predicted that the slope of the relationship between predation rate and in-stream age would be strongly negative. That is, bears should preferentially kill younger energy-rich salmon. In habitats that do not facilitate choice (deeper, more complex streams), the slope of the relationship should become less negative (bears will be less selective as more effort is necessary to capture salmon), zero (random predation; bears show no selectivity), or even positive if in-stream age positively influences capture success.

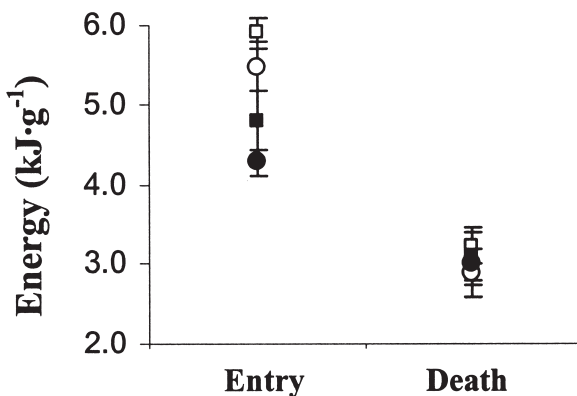


Fig. 1. Changes in energy content (kJ g^{-1} wet mass) from stream entry (1st day in stream) to senescent death (about 10–21 days after stream entrance at Himmel Creek and 10–25 days at Pick Creek) for male (■) and female (□) pink salmon spawning in Himmel Creek, and male (●) and female (○) sockeye salmon spawning in Pick Creek. Data were obtained using proximate analysis of tagged fish of known in-stream ages (Hendry and Berg 1999, Gende 2002). Values for whole Pick Creek sockeye salmon were calculated by multiplying the energy values of soma and gonad tissues by their body weight proportions (females: 80% soma, 20% gonads; males: 95% soma, 5% gonads) and adding the resulting two values together.

Material and methods

General procedures

Bears are prone to disturbance and may alter their natural foraging behavior in response to the presence of humans (Reinhart and Mattson 1990, Chi 1999).

However, to test our hypothesis, large sample sizes are necessary because bears exhibit considerable individual variation in factors that influence foraging behavior (e.g. social and reproductive status, age, and experience, Fagen and Fagen 1994). Therefore, direct observations of bears are not necessarily the most powerful or appropriate technique for studying prey choice. To minimize disturbance to bears while maximizing samples sizes, our primary approach was to examine the fate of salmon (of known in-stream age) on a daily basis, thereby inferring foraging decisions by bears. Behavioral inference of predators by examining prey has been successfully employed in many foraging studies (Werner et al. 1983, Stephens and Krebs 1986). We supplemented these large data-sets of tagged salmon with some observations of bears at one of our sites and at several nearby streams.

Study sites

We studied the spawning runs of sockeye salmon and pink salmon, two abundant and widespread species (Groot and Margolis 1991) that commonly spawn in small streams where bears forage (Dickerson et al. 2002, Quinn et al. 2003). Our study streams were located at sites with very little human influence, and with healthy brown bear and salmon populations.

Hansen Creek (59°32'127"N, 158°70'161"W) is a small, shallow, spring-fed stream (Table 1), flowing into Lake Aleknagik in the Wood River system in southwestern Alaska (for habitat data see Marriott 1964, for a map see Quinn et al. 2001b). Hansen Creek provides virtually no refuge from predation because it lacks pools or large woody debris, and the water is so shallow that some salmon even die of stranding (Quinn and Buck 2001, Quinn et al. 2001b). Pick Creek (59°33'00"N, 159°04'18"W) is another spring-fed stream in the Wood River system, but is wider and deeper than Hansen Creek, with some pools but little woody debris (Hendry 1998, Table 1). Like Hansen Creek, water level, temperature, and discharge are relatively constant when sockeye salmon are present (Hendry 1998). Both creeks are about 2 km long and support similar numbers of

spawning sockeye salmon between late July and mid-late August (T. Quinn and R. Hilborn, unpubl.). Himmel Creek is located in southeastern Alaska, on northeast Chichagof Island, approximately 70 km west of Juneau (Gende et al. 2001, Dickerson et al. 2002). Himmel Creek is, on average, slightly shallower than Pick Creek but has alternating riffles and deep pools, and large amounts of woody debris. Flows vary considerably over the course of the spawning season, according to the amount of precipitation. Pink salmon spawn in Himmel Creek from late July until early September.

Previous work in a series of streams in the Wood River system (including Hansen and Pick) and elsewhere in southwestern Alaska demonstrated that the probability a fish is killed by bear increases with decreasing stream size (Quinn and Kinnison 1999, Quinn et al. 2001a). Direct observations on Himmel and other creeks in southeastern Alaska showed that deep pools and woody debris provided escape opportunities for salmon (Gende 2002). More effort (time) was necessary for bears to capture fish as water depth and the frequency of large woody debris increased.

Salmon reproductive biology

Predation by bears is virtually non-existent until salmon enter their spawning streams from lakes (Hansen and Pick creeks) or the ocean (Himmel Creek). After entering a stream, female salmon obtain and prepare nest sites (redds) while males compete for access to females (Foote 1990). After depositing their eggs in the gravel, females defend their nest site from other females (Quinn and McPhee 1998). Males may continue to court the same female or may leave to search for and court other ripe (egg-carrying) females (Foote 1990). Pink and sockeye salmon are semelparous and all die after days to weeks on the spawning grounds. The average duration of in-stream life for fish not killed by predators is highly dependent on the date of stream entry and ranges from 5–15 days in Hansen Creek (McPhee and Quinn 1998), 10–25 days in Pick Creek (Hendry et al. 1999), and 8–22 days in Himmel Creek (Dickerson et al. 2002). From the time when salmon enter streams until they die, males and females typically lose up to 80–95% of their lipid reserves and 40–80% of their total energy (Gilhousen 1980, Hendry and Berg 1999). This pattern appears universally true for Pacific salmon and has been directly confirmed in Pick Creek (Hendry and Berg 1999, Hendry et al. 1999) and Himmel Creek (Fig. 1, Gende 2002).

Determination of in-stream age

Our study was conducted over 2 years at Pick Creek (1995–1996), 3 years at Hansen Creek (1999–2001), and

Table 1. Characteristics of our three study streams. Values were obtained in habitat surveys for Himmel Creek (Dickerson et al. 2002), Hansen Creek (Marriott 1964), and Pick Creek (Marriott 1964).

Creek	Hansen	Himmel	Pick
\bar{x} depth (cm)	10.0	30.3	33.3
\bar{x} width (m)	4.0	6.4	7.7
Spawning area (ha)	0.83	0.21 ^a	1.54

^aSpawning habitat in Himmel Creek was limited by a large tangle of woody debris in 1997 and 1998. Part of this spawning barrier was washed out in 1999 allowing salmon access to another 470 m of stream in 1999 and 2000.

4 years at Himmel Creek (1997–2000). Salmon were caught by beach seine or dip net near the mouth of the creek, anesthetized, and tagged with an individually coded 3-cm disc tag placed in the musculature below the dorsal fin. These capture and tagging procedures are standard for salmon and have no obvious effects on their behavior, vigor, or life span (Quinn and Foote 1994; Hansen: Quinn and McPhee 1998; Pick: Hendry et al. 1999, 2001; Himmell: Dickerson et al. 2002).

Each stream was walked daily to determine the in-stream age of each tagged fish by recording the day it entered the stream and its presence on subsequent days ('in-stream age' equals the number of days a fish had spent in the stream). When a tagged salmon was found dead, we recorded its mode of death: 'senescent' or 'bear-killed' (Quinn and Buck 2001, Quinn et al. 2001b). 'Senescent' dead fish were distinguished by emaciated bodies, fungus, scars from fighting, and abraded skin from digging. Bear-killed fish were distinguished by severe wounds, typically in the belly of females and the dorsal hump and cranial area of males (Gende et al. 2001). Tags almost always remained attached to the carcass because bears only partially consumed each fish (Gende et al. 2001). Although some birds scavenge carcasses at these creeks, no other animals at these streams are capable of inflicting bear-like wounds. Thus we are confident that salmon classified as "bear-killed" based on the appearance of their carcasses were indeed killed by bears (Gende et al. 2001, Quinn and Buck 2001, Gende 2002). More information on the tagging procedures and daily surveys is provided for Hansen Creek in Quinn et al. (2001b), Pick Creek in Hendry et al. (1999, 2001), and Himmel Creek in Dickerson et al. (2002).

If a salmon was dead on the first day it was seen in the stream, it was recorded as having lived for 1 day, even though some may have entered only a few hours before the survey. This will underestimate predation rates on fish aged one day but this sampling bias was small and unavoidable. If a fish was seen in the stream for at least two days but never thereafter, we assumed it was killed by bears and carried into the forest, which is common (Reimchen 2000, Gende et al. 2001, Quinn et al. 2001b). Moreover, salmon that enter a creek rarely leave the creek to spawn elsewhere. The assumption that missing fish were killed rather than un-noticed was validated at these sites by comparing the size distributions and in-stream life spans of fish known to be killed by bears, died of senescence, or went missing (Quinn et al. 2001b).

Data analysis

We calculated predation rates on fish that had spent d days in the stream (where $d = 1, 2, 3, \dots, T$) as:

$$y_d = \frac{k_d}{a_d} \quad (1)$$

where y_d is the observed predation rate, k_d is the number of fish killed by bears (aged d), and a_d is the total number of tagged fish alive aged d (i.e. available to bears). We then calculated the expected (predicted) number of fish killed at each age using a linear model for each fish age (d):

$$\hat{y}_d = md + b \quad (2)$$

where \hat{y}_d is the predicted predation rate on fish that spent d days in the stream, m is the slope, and b the intercept. We had no a priori expectation that the data would follow a certain distribution so we used a linear model because (1) energy loss in salmon (and thus reward to bears) decreases with in-stream age (Hendry and Berg 1999, Fig. 1), and (2) to keep the number of parameters in the model small and easily interpreted. For this model, the slope represents the change in predation rate relative to in-stream age. The predicted number of kills on each day can then be calculated as:

$$\hat{k}_d = \hat{y}_d a_d \quad (3)$$

We fit the linear models to the data using maximum likelihood estimates. We assumed the probability distribution of the data followed a negative binomial distribution. In tagging studies where count data are collected, a Poisson distribution is commonly used but the negative binomial distribution may fit the data better by including a dispersion parameter, p , which represents the variance (Hilborn and Mangel 1997). The negative binomial distribution approximates the Poisson distribution if the data are not overly dispersed (Hilborn and Mangel 1997). We calculated the log-likelihood (l) of the predicted number of kills given the observed number of kills and the dispersion parameter:

$$l(k_d | \hat{k}_d, p) = \ln \left(\Gamma \left(\frac{\hat{k}_d}{p-1} + k_d \right) \right) - \left[\ln \left(\Gamma \left(\frac{\hat{k}_d}{p-1} \right) \right) + \ln(k_d!) \right] - \frac{\hat{k}_d}{p-1} \ln(p) + k_d \ln \left(\frac{p-1}{p} \right) \quad (4)$$

where Γ is the gamma function (Hilborn and Mangel 1997).

The total log-likelihood (L) for the negative binomial will be the sum of the individual log-likelihoods generated for each age (d):

$$L_d = \sum_{d=1}^{d=T} l_d \quad (5)$$

Thus the total log-likelihood represents how well a model fits the data, where smaller (more negative) likelihoods correspond to a poorer fit.

We first tested the hypothesis that the parameters m , b , and p were the same across streams (i.e. the relationship between predation rate and in-stream age did not vary among sites). We then considered each site separately, asking whether the relationship between predation rate and in-stream age differed between sexes or among years. For example, each stream potentially had different values for each parameter (m_{stream} , b_{stream} , and p_{stream}), and each sex and year potentially had different values for each parameter within a stream ($m_{\text{sex,year}}$, $b_{\text{sex,year}}$, and $p_{\text{sex,year}}$). We used likelihood ratio tests to see if adding parameters (by first assuming sites, sexes, or years were the same) resulted in significant increases in likelihood (better fit). For likelihood ratio tests, the difference in total likelihood of two models, one nested in another, are assumed to be Chi-square distributed, with the difference in the number of parameters between models constituting the degrees of freedom (Hilborn and Mangel 1997). Statistical significance was accepted at $P < 0.05$.

We have thus far assumed that bears had access to many salmon, ranging from high-energy fish that had just entered the stream to nearly dead fish with depleted energy stores, thereby providing an opportunity for bears to choose among all prey types. However, the availability of salmon of different in-stream ages will vary through the course of the run; most will be young and energy rich early in the run but old and energy poor late in the run. We accounted for this effect by comparing the in-stream age structure of salmon available to bears with the age structure of salmon killed by bears over the course of the spawning season. To do so, we first pooled fish into 4 categories of in-stream life, corresponding to 3 day (Hansen, Himmel) or 4 day increments (Pick). For example, at Hansen Creek fish were categorized as having spent 1–3 days in the stream, 4–6 days, 7–9 days, and 10+ days. These categories provided large cells for statistical comparison and are biologically relevant because female salmon tend to spawn all of their eggs within the first 3 days (McPhee and Quinn 1998, Quinn et al. 2001b), thereby ‘losing’ much of their available lipid and energy (Gende 2002).

Results

A total of 1933 salmon were tagged and observed in the three creeks: 474 (158 females, 316 males) at Hansen Creek, 903 (495, 408) at Himmel Creek, and 556 (281, 275) at Pick Creek. Of these, 1243 (64.3%) were killed by bears, 639 (33.1%) died of senescence, and 51 (2.6%) died for other reasons (e.g. gull attacks or stranding). This latter group was excluded from the analysis. The

relationship between predation rate and in-stream age differed among sites. Adding site-specific parameters (9-parameter model) resulted in a significantly better fit to the data ($L = -145.3$) compared with the basic 3-parameter model ($L = -200.1$) of common slope, intercept and dispersion parameters ($\chi^2_6 = 453$, $P < 0.001$, Fig. 2). At Hansen Creek, predation rates were between 11% and 40% for fish that had been in the stream for 3 days or less but declined thereafter; fish aged 12 days or older were avoided by bears and suffered little predation. Consequently, the model slope was strongly negative ($m_{\text{Han}} = -0.013$).

In contrast, older fish were subject to increasingly higher rates of predation at both Pick and Himmel creeks. At Himmel Creek, predation rates were almost zero for fish during their first few days in the stream, but increased with fish age; predation rates for fish aged 12 days or older ranged between 25–40% (Fig. 2). Consequently, the best-fit slope was nearly identical in magnitude to Hansen Creek but was positive ($m_{\text{Him}} = 0.012$). Likewise, the predation rate at Pick Creek gradually increased with in-stream age ($m_{\text{Pic}} = 0.002$), although not as dramatically as at Himmel. Only fish living to 25 days or more were subject to predation rates $> 8\%$.

Because of differences among sites, we repeated our model building procedure to test whether adding sex- or year-specific parameters significantly improved the fit. At Hansen Creek, the best-fit model included year-specific slope, intercept, and dispersion parameters (Table 2). Adding sex-specific parameters did not significantly improve the fit over a basic model of common slope, intercept, and dispersion parameters ($\chi^2_3 = 1.0$, $P > 0.75$), nor over a model with year-specific parameters ($\chi^2_9 = 4.8$, $P > 0.75$, Table 2). Likewise, at Himmel Creek the best-fit model was one that included year-specific parameters ($\chi^2_9 = 30.59$, $P < 0.001$, Table 2). Adding sex-specific parameters did not significantly improve the fit over a basic model of common parameters ($\chi^2_3 = 3.17$, $P > 0.25$), nor over a model with year-specific parameters ($\chi^2_{12} = 8.16$, $P > 0.75$). These results show that predation rates at these sites differed among years but not between sexes.

At Pick Creek, however, models containing sex-specific parameters significantly improved the fit of the data ($\chi^2_3 = 23.6$, $P < 0.001$, Table 2), but the relationship between in-stream age and predation rate did not differ among years ($\chi^2_3 = 6.3$, $P > 0.5$). To consider whether males or females experienced higher rates of predation, we re-fit the model by setting the intercept equal to 5 days. In other words, we estimated the predation rate for males and females that had been in the stream for 5 days. Males were subject to predation rates an order of magnitude greater than females in both 1995 ($m_{\text{males}} = 0.00751$ vs $m_{\text{females}} = 0.00098$) and 1996 (0.00431 vs

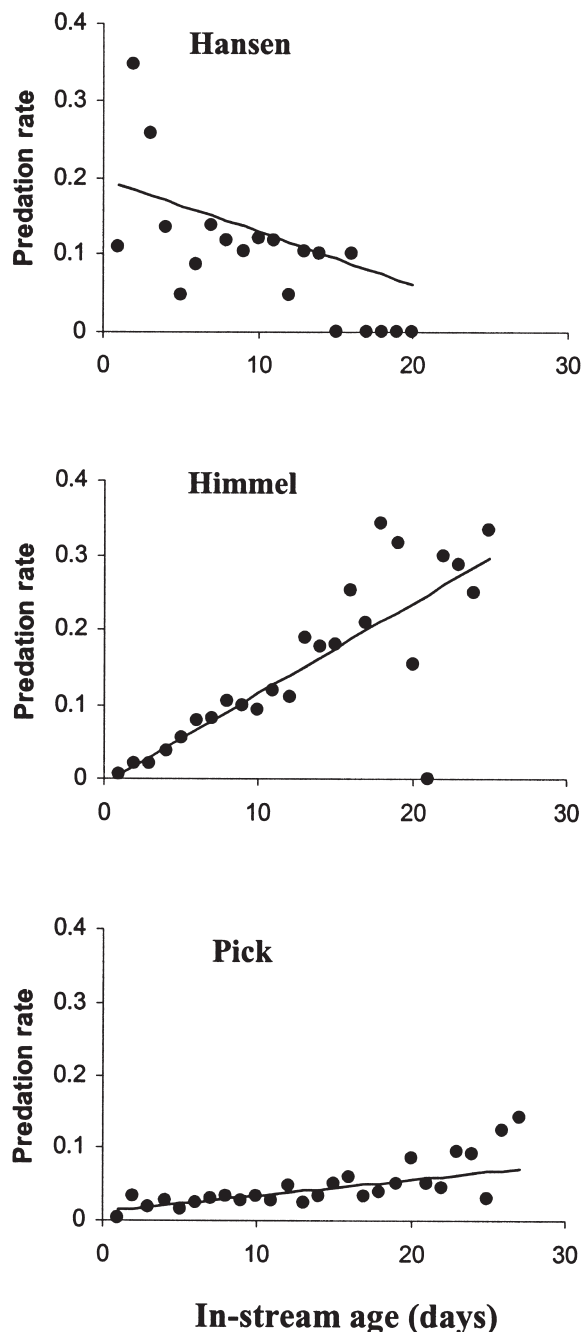


Fig. 2. Predation rate (proportion of available fish killed) relative to in-stream age at three study streams. Circles represent the observed data and lines represent the best fit using a linear model and maximum likelihood estimates.

0.00094, Fig. 3). Similar results occurred when intercepts were set to in-stream ages of 10 and 15 days.

Results were generally similar after accounting for the in-stream age structure of bear-killed versus available fish. At Hansen Creek, the proportion of young fish (aged 1–3 days) killed by bears was higher than that

expected by chance over the entire course of the spawning season. For example, nearly 69% of the fish killed by bears from August 1st through August 8th in 1999 were aged 1–3 days, even though only an average of 15% of the fish available to bears fell within that age class (Fig. 4, top panel). At Pick Creek, the age structure of bear-killed salmon generally reflected the age structure of available fish throughout the run (Fig. 4, middle). This suggested that choice was nearly random, which was similar to the previous conclusion that predation rates were not strongly influenced by in-stream age (Fig. 2). At Himmel Creek, the proportion of young fish (aged 1–3 days) killed by bears was lower than that expected by chance. For example, from August 25th until September 2nd, at least 20% of the salmon population had been in Himmel Creek 3 days or less yet bears did not kill any young fish during this period (Fig. 4, bottom panel). In contrast, between August 25th and September 1st, almost 48% of the fish killed by bears were aged 7+ days though only 14% of the available fish were that old.

Discussion

Many diet studies of foraging organisms have revealed 'diet preferences', i.e. the frequency of prey types included in a diet differs from their relative frequency in the environment (Sih and Christensen 2001). However, these non-random diets may be a function of any combination of the steps in the predation event, including elevated encounter, attack, capture, or consumption probabilities (Scheel 1993). For example, if two different prey types are equally abundant and offer similar energetic rewards to a predator but one is encountered more often (due to behavioral or habitat differences among prey types), the predator's diet may be non-random with respect to this prey type. That is, the predator's diet may be non-random, but may not necessarily reflect active choice. Our hypothesis was that at the smallest streams (habitats facilitating choice), bears should selectively kill younger, energy-rich salmon, i.e. the diet preferences should be a function of elevated attack probabilities (active choice by bears) rather than elevated encounter rates or capture success. In contrast, when habitats do not facilitate choice, bears might show lower preference for younger fish, due to elevated effort necessary to capture them. Thus, to demonstrate that the mechanism resulting in elevated predation rates on high-energy salmon at Hansen creek was active choice by bears, and to understand why these results differed at the larger streams, it is necessary to demonstrate that predation rates reflect active choice in small streams but reflect elevated encounter or capture probabilities at larger streams.

Table 2. Likelihood estimates for models of predation rate relative to in-stream age. Listed is the general model layout, number of parameters used to estimate likelihood, and the corresponding likelihood estimates. For example, Pick Creek was surveyed in 1995 and 1996 so year-specific slope, intercept, and dispersion parameters yields 6 parameters in the model. Larger likelihood corresponds to a better fit to the data.

Model	Hansen		Himmel		Pick	
	No. parameters	L	No. parameters	L	No. parameters	L
Model I. Years and sexes the same	3	−197.5	3	−322.9	3	−237.7
Model II. Sexes different, years the same	6	−196.5	6	−319.8	6	−214.0
Model III. Years different, sexes the same	9	−160.1	12	−292.3	6	−231.3
Model IV. Years and sexes different	18	−155.3	24	−284.2	12	−193.0

Predation in habitats that facilitate choice

At Hansen creek, predation rates were clearly highest on young energy-rich salmon; salmon approaching senescent death were avoided altogether. We have already discussed how bears are able to perceive variation in energy content because fish of different in-stream ages have different physical appearances (Brett 1995). Here we highlight several characteristics of salmon spawning behavior and habitat attributes that suggest predation rates in this creek reflect active choice by bears rather than differences in encounter probability or capture success.

First, for the majority of the salmon run, bears were likely to encounter salmon that differ in their energy content. As fish enter the streams over the course of spawning run, salmon of all in-stream ages become distributed across all available spawning habitat as females construct and defend their redds and males

court females (Hendry et al. 2001). Second, bears forage for salmon by walking up or downstream in the water or on the stream banks, often covering the entire stream length during a foraging bout (Gende 2002). Bear-killed salmon were found throughout the stream during the whole season and thus bears searched the entire stream daily and would encounter fish varying in energy content. Third, Hansen Creek has no deep pools, undercut stream banks, or tangles of woody debris that could serve as refuges from predation, and thereby influence encounter or capture rates. Young energy-rich fish were not strongly geographically or temporally segregated (for the majority of the run) from energy-poor salmon. Thus, bears were likely to encounter both high- and low-energy salmon throughout much of the spawning season. Even during the final days of the salmon run when most available fish were low-energy, bears disproportionately killed the few remaining high-energy salmon.

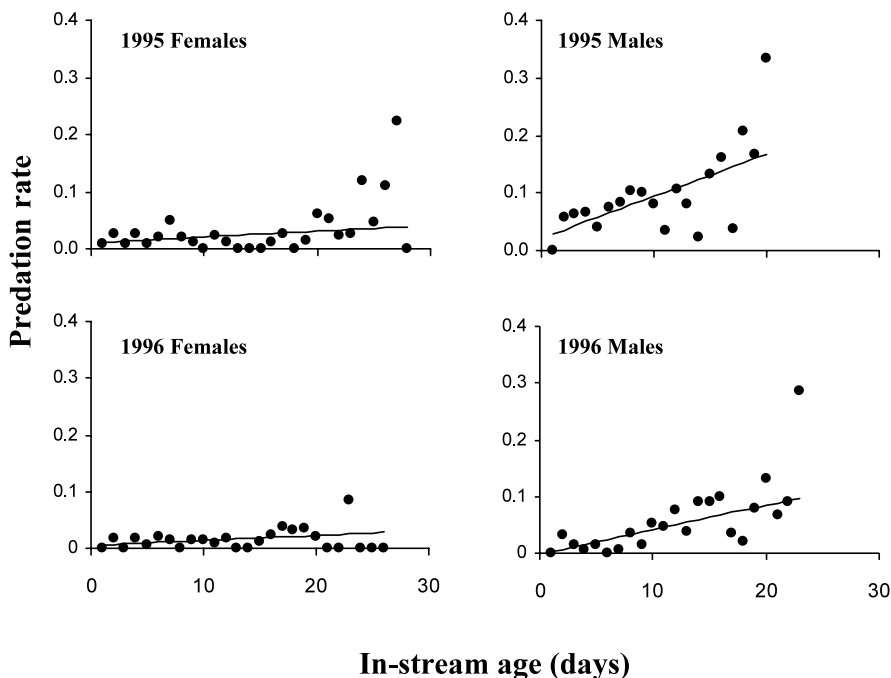


Fig. 3. Predation rate relative to in-stream age for male and female sockeye salmon at Pick Creek. Circles represent the observed data and lines represent the best fit using a linear model and maximum likelihood estimates.

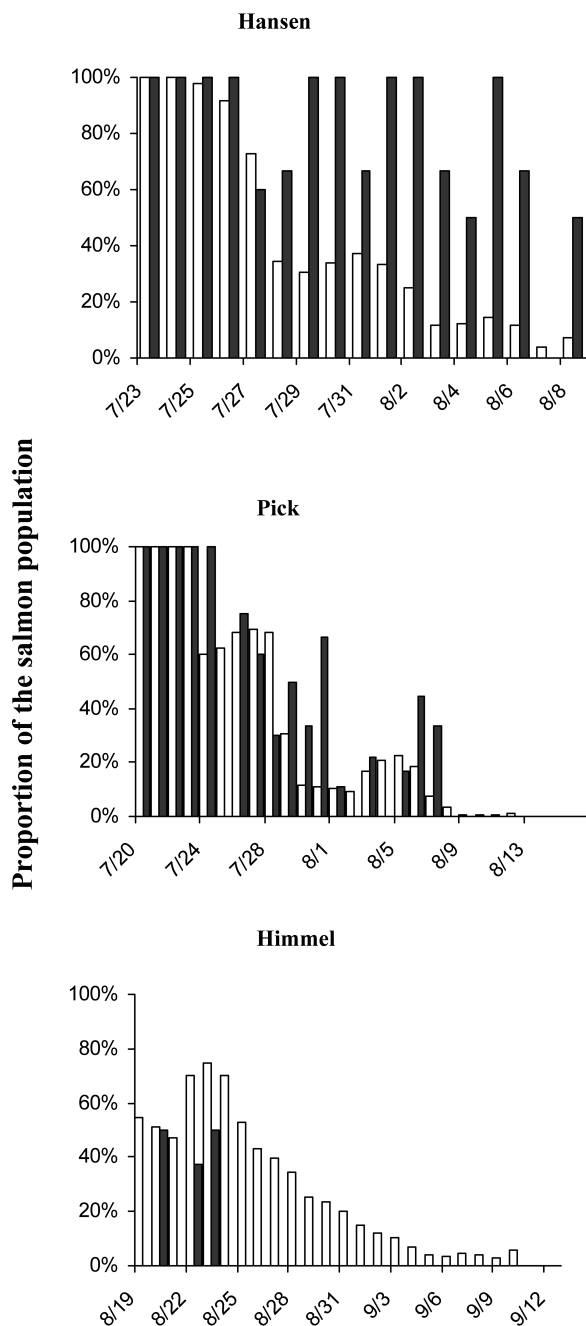


Fig. 4. Proportion of the salmon population (□) that were aged 1–3 days (Hansen, Himmel) or 1–4 days (Pick) during each day of the salmon spawning season in 1999 at Hansen Creek (top panel), 1995 at Pick Creek (middle panel), and 1998 at Himmel Creek (bottom panel). Closed bars (■) represent the proportion of the fish that were killed on that day that fell within these age brackets. For example, on July 31st at Hansen Creek, only 36% of the salmon that were available to bears were 1–3 days old, but 100% of the fish killed by bears on that day were 1–3 days old. We arbitrarily chose these years and pooled the sexes for illustrative purposes. Other years showed similar patterns.

In addition, salmon are sufficiently available at Hansen Creek that bears can choose not to attack older fish and still have many salmon available to them. There were far more salmon than bears could or would kill: about 100 were killed each day whereas several thousand were available during much of the run (Quinn et al. 2003). This not only means that bears had many salmon to choose among but also that not all “preferred” young fish were killed. At Hansen Creek, fish that survived for several days were then generally avoided by bears thereafter. In several cases we observed older salmon (4+ days) living until senescent death (9+ days) while neighboring (spawning 1–3 meters away) young salmon were killed.

Another observation further suggests that selective predation on younger salmon reflects active choice rather than differential encounter or capture probability. As salmon age and their stored reserves of lipid and protein decrease, the ability to sustain rapid swimming speeds (and presumably avoid predators) decreases (Webb 1975). We have exposed pairs of fish to simulated bear ‘attacks’ and found that fish that have completed spawning or those close to senescent death reacted slower, fled a shorter distance (if at all), and returned to spawning sites faster than fish that had spent fewer days in the stream (S.M. Gende and T.P. Quinn, unpubl.). Moreover, the activity rates of female salmon in Hansen Creek are known to decrease with in-stream age (Quinn and McPhee 1998). Capture success should, if anything, increase as energy reserves in salmon are depleted, thereby elevating predation rates on older fish, in contrast to our results.

Supplemental direct observations of foraging bears corroborated our conclusion that bears selectively kill young salmon when streams are shallow. At Bear Creek, about 5 km from Himmel Creek, bears were observed gradually walking upstream and selectively attacking young ripe salmon. In several cases, a spawned-out salmon became stranded on a gravel bar while fleeing a nearby foraging bear, yet the bear continued to search for and attack younger fish (Gende 2002). When stream depths averaged 9 cm (comparable to Hansen Creek), the number of young, energy-rich fish attacked by bears was disproportionately higher than the age structure of available fish in that reach of stream (Gende 2002). When stream flows were elevated, bears needed more time to capture salmon and disproportionately captured fish that were closer to senescent death (Gende 2002).

Post-capture consumption by bears is also consistent with the hypothesis that bears make foraging decisions to elevate their lipid intake. In an analysis of 22 000 salmon carcasses over ten years at five spawning streams, bears selectively consumed body parts that were highest in lipid density (Gende et al. 2001, Gende 2002). Thus, bears modify both their capture and consumption choices in order to maximize rates of energy intake.

Predation in habitats that do not facilitate choice

In contrast to Hansen Creek, predation rates increased with in-stream age at the wider, deeper and more structurally complex Himmel and Pick creeks; older fish were clearly subject to higher predation rates than younger fish. This result held after accounting for variation in in-stream age structure through the spawning season. Without direct observation, we cannot say why preferences shifted to older salmon. Similar to Hansen Creek, bears at Himmel and Pick creeks encountered many fish of all ages while walking the stream (we found bear-killed salmon throughout the stream at both sites), and young energy-rich salmon were found throughout the stream spawning near energy-poor salmon. Thus encounter rates should largely be independent of fish age in these two streams. Instead, diet preferences of bears may have shifted to older fish in response to the elevated effort (costs) necessary to capture young energy-rich salmon at these larger creeks.

For example, larger streams generally equate to more effort to capture salmon. The amount of time necessary to capture a fish at McNeil River Falls, a large Alaskan river, was about three times greater than that at smaller streams in southeast Alaska (comparison of data in Egbert and Stokes 1976, Gende 2002), which is why predation rates were found to have a highly significant negative relationship with stream size (Quinn and Kinnison 1999). At Bear and Himmel Creeks, the time necessary to capture a salmon tripled when flows were high following heavy precipitation, irrespective of sex, reproductive, or social status (dominant, sub-ordinate) of the bears. Thus, the net benefit of capturing any salmon (regardless of energy content) is lower at the larger streams compared to the smaller streams. By extension, bears should be less selective than at the smaller streams, i.e. the relationship between predation rate and salmon age should be less negative than at the smaller streams.

However, young energy-rich salmon are also more vigorous. Whereas at Hansen Creek the uniformly shallow depths reduced or eliminated the ability of salmon to elude capture (salmon often become stranded when fleeing bears at Hansen creek), the deeper and wider Pick and Himmel Creeks provided more escape opportunity. Thus given an attack, high-energy salmon are probably more difficult to capture than the less vigorous low-energy salmon at the larger streams whereas they are equally as likely to be captured at Hansen Creek. The elevated capture success of low-energy salmon, in addition to the elevated effort necessary to capture all fish at the larger streams, produced the elevated predation rates on the low-energy salmon at the larger streams. By 'preferring' younger salmon at the small streams (where effort doesn't vary with salmon energy content) but older salmon at the larger streams

(where effort decreases with low-energy salmon) bears may be maximizing their energy intake per unit effort at both types of habitats.

Differences in capture success may also explain why male salmon experienced greater rates of predation than females, but only at the deepest creek (Pick Creek). Sockeye salmon are sexually dimorphic, with males, on average, both longer- and deeper-bodied than females (Quinn and Foote 1994, Hendry and Berg 1999). At Pick Creek, average-sized males exceeded average-sized females by 36.4 mm in length and 38.4 mm in body depth, which should make male salmon easier to see or capture and therefore more vulnerable to predation. Indeed, selective predation has been recorded in these and other streams; larger fish and males generally experienced greater mortality rates than smaller fish and females (Quinn and Kinnison 1999, Ruggerone et al. 2000, Quinn et al. 2001b).

We also found that the relationship between in-stream age and predation rates differed among years at Hansen and Himmel, but not at Pick. This may be due to the relative magnitude in variation of spawner densities among years at the respective sites. For example, at Hansen and Himmel Creeks, spawner densities varied among years by 75% and 66%, respectively, whereas they only varied by 29% at Pick Creek. However, the nature of the relationships between in-stream age and predation rate were consistent among years (the slope changed but the sign was consistent) within each stream, indicating that the underlying patterns were related to differences between streams (probably habitat). It is noteworthy that the apparent selectivity of bears for newly arrived salmon was evident over a ten-fold range of densities at Hansen Creek.

Conclusions

Although our results clearly showed that bears preferentially killed young high-energy salmon at a small shallow stream but more frequently captured low-energy salmon at larger, more complex streams, it is necessary to increase replication among streams sizes and control for species, collect more direct observational data to fully assess the costs associated with capture and consumption of salmon, and account for variation in behavior among individual bears (Fagen and Fagen 1994, Hayes and Jenkins 1997). For example, social dominance influences how much time is spent on the stream by individual bears (Egbert and Stokes 1976, Chi 1999, Gende 2002). As the number of bears using a stream increases, the average foraging bout (uninterrupted time pursuing and consuming prey, Lucas 1983) will decrease. Should foraging bouts become exceedingly short, the number of high-energy salmon missed while handling older, low-energy fish will increase, thereby influencing

whether low-energy fish should be included in the diet (Lucas 1983). Scavenging dead salmon when live salmon are available (Quinn and Buck 2000) may in part reflect these aspects of bear behavior. Sub-ordinate bears may only have a short time to acquire a salmon before they are displaced from a stream. With little time available they may select only prey types that need little effort to acquire (senescent dead salmon). Our samples sizes may have been large enough to account for individual differences among bears to reveal the overall foraging behavior of bears when fishing for salmon.

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